

RECOVERY FROM SEXUAL SATIETY IN MALE RATS

by

SALLY BOLCE JACKSON

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RECOVERY FROM SEXUAL SATIETY IN MALE RATS

By

Sally Bolce Jackson

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Although it has long been known that a 15-day rest period is sufficient to provide complete recovery from the effects of sexual satiety in male rats, and that a 6-day rest period is apparently not sufficient, evaluation of recovery during the interval from 6-15 days has not previously been undertaken.

In this study 18 rats were tested after each of six periods of recovery: 3, 6, 9, 11, 13, and 15 days following satiety. Several methodological controls were employed. Copulatory experience, including satiety, was given to sexually naive subjects prior to the experiment. Because of high variability among individuals relative to within individuals, the within-subjects design was used. In order to standardize the exhaustion from which recovery was measured, subjects were allowed full recovery and then satiated to a standard criterion prior to each test.

Different rates of recovery were found for different measures of copulatory behavior. While most measures recovered their normal levels by 6 days following satiety, the postejaculatory interval following the second ejaculation still was longer than normal even after 9 days of rest. No changes were seen in intromission frequency. The effect of prior satiety on other within-series measures was seen more clearly in the second and third series than in the first.

The finding that the postejaculatory interval recovers at a different rate than other measures is consistent with models which propose at least two separate mechanisms underlying the normal pattern of copulatory behavior in rats. The finding that the latencies to begin copulation do not recover from the effects of satiety at the same rate as the postejaculatory interval lends support to the idea that these measures do not reflect the operation of the same mechanism.

An unexpected finding was that changes in copulatory behavior occurred over the course of the experiment in the satiety sessions preceding each experimental test. Because of the randomization procedure employed, no confounding interactions were found between running orders and recovery intervals.

INTRODUCTION

The central importance of reproductive processes in evolution is illustrated by the very definition of a species as "a reproductively isolated aggregate of interbreeding populations." Reproduction is a key element in the concept of biological fitness, which is measured in terms of the number of viable, fertile offspring an individual leaves.

Of reproductive processes, the most versatile and far-reaching in its effects is behavior. "Behavior is perhaps the strongest selection pressure operating in the animal kingdom. . . . A shift into a new niche or adaptive zone is almost without exception initiated by a change in behavior. The other adaptations to the new niche, particularly structural ones, are acquired secondarily. . . . The precedence of behavior over structure is most easily demonstrated with respect to courtship patterns in birds and the accumulation of morphological characteristics that make the courtship more conspicuous and stimulating" (Mayr, 1970, pp. 387, 363, 364).

Courtship and reproductive behavior provide the largest and most important class of reproductive isolating mechanisms, which function to prevent the wastage of gametes and constitute the most indispensable step in speciation.

Because of the intimate relationship of mating behavior with fitness, copulatory behavior can provide a good focus for the study of gene action. As Caspari has stated: "Since the possibility of the transfer of genes by an individual depends on its success in mating, activities leading to success in mating, as far as they are influenced by genes, may form a strong component of selective value. It is for this reason that workers interested in evolution have carefully studied the influence of particular genes on sexual behavior and the consequent success in mating" (Caspari, 1965, pp. 47-48). Indeed, apparently small variations in mating behavior can have major consequences for reproductive success. Male rats, for example, normally effect several discrete insertions prior to ejaculation. The probability of pregnancy occurring is directly related to the number of these pre-ejaculatory intromissions a female receives (Wilson, Adler & LeBocuf, 1965; Adler, 1969).

Copulatory behavior can also provide an excellent focus for comparative study in the laboratory. Patterns of copulatory behavior show substantial variations among species, while the pattern within a species tends to be highly stereotyped. Large individual differences may exist in quantitative measures, but the general pattern of behavior for individuals within a species is highly similar. These highly differentiated species-typical patterns provide good material for clear-cut comparative analysis.

Copulatory behavior has also been approached as a consummatory response for study under the rubric of motivation. Sex has been viewed as a primary drive, along with hunger and thirst, and a certain amount of research has been published measuring the strength of the sex drive in an obstruction box (e.g., Warner, 1927) and concerning the reward value of copulation in the context of drive-reduction theories (e.g., Sheffield, Wulff & Backer, 1951). Interpretation of a number of the earlier studies of rats suffered from a lack of adequate description of the naturally occurring pattern of copulatory behavior in rats (cf. Stone & Ferguson, 1940).

Beach (1956) clarified several problems involved in the definition and classification of sex as a drive, and the great bulk of the research since then has been directed toward providing descriptive information on copulatory behavior in the species studied and toward an understanding of the factors governing the temporal patterning of the behavior and of the neural and hormonal mechanisms involved.

While the catalogue of species studied is growing steadily, the species in which copulatory behavior has been most often studied is the laboratory rat, Rattus norvegicus. This is not inappropriate for many of the kinds of research questions one can ask, since the rat is an ideal species for systematic analysis. Large numbers of subjects are readily available, and there is an abundance of data on the effect of

myriad experimental manipulations and on the controls needed in research. Copulatory behavior is stable and reliably reproducible in the laboratory, yet it is sensitive to a wide variety of manipulations. The extensive literature includes some effects of developmental variables, such as early experience (Kagan & Beach, 1953), of physiological interventions, such as cortical ablations (e.g., Larsson, 1962; 1964), and of various drugs (e.g., Whalen & Luttge, 1970; Salis & Dewsbury, 1971) as well as of numerous other kinds of variables.

The remainder of this section will consist of a description of the pattern of copulatory behavior in rats and the measures commonly used in studying it, a review of existing literature on a particular aspect of the behavior--recovery from sexual satiety, and a statement of the problem to which the present study is addressed.

Description of Copulatory Behavior in Rats

Laboratory rats display a copulatory pattern involving multiple intromissions, multiple ejaculations, no thrusting during intromissions, and no lock. This is pattern 13 in Dewsbury's classification scheme and is found fairly commonly among muroid rodent species (Dewsbury, 1972).

A male rat given access to a receptive female shows three major copulatory responses, which can be readily distinguished by the observer: mounts, intromissions, and ejaculations. During a mount the male clasps the flanks of

the female with his forepaws and moves his pelvic region in several rapid thrusts without vaginal insertion. This takes less than a second.

An intromission consists of the same palpation with forepaws and shallow pelvic thrusting, but the final, deep thrust achieves vaginal penetration. The penetration lasts a fraction of a second and is terminated by a distinctive forceful, rapid dismount. Intromission is followed by autogenital grooming.

After about 10 intromissions, spaced about 1 min apart, ejaculation occurs. The male mounts, gains vaginal penetration, and displays a spasm of the hindquarters. After ejaculation the male remains quite still for several seconds, tightly clasping the female's flanks. Then he slowly releases his grasp. This completes the first "series"--the group of mounts and intromissions leading up to and including the ejaculation.

A postejaculatory interval of about 5 min elapses before the male once again gives chase and begins a second series which culminates in a second ejaculation. The second ejaculation typically occurs after fewer intromissions than the first, and the intromissions of the second series are usually spaced closer together than those of the first. The postejaculatory period of inactivity increases regularly following each successive ejaculation. With a criterion for satiety of 30 min without an intromission, six or seven

ejaculations are typically found before the male ceases to copulate.

It is convenient to discuss these changes in terms of the standard measures of copulatory behavior. The following is a list of these measures with their definitions: mount latency (ML)--the number of seconds from introduction of the female to the first mount, with or without intromission; intromission latency (IL)--the number of seconds from the introduction of the female to the first intromission; ejaculation latency (EL)--the time in seconds from the first intromission of a series to the ejaculation; mount frequency (MF)--the number of mounts (without intromission) in a series; intromission frequency (IF)--the number of intromissions in a series; the mean interintromission interval (MIII)--the mean interval separating the intromissions of a series, derived by dividing EL by IF; the postejaculatory interval (PEI)--time in seconds from an ejaculation to the first intromission of the next series; and ejaculation frequency (EF)--the number of ejaculations obtained in the test. One further convention will facilitate discussion. The series to which a given measure refers can be denoted by appending the number of that series with a hyphen. For example, IF-2 refers to the number of intromissions in the second series. PEI is designated by the number of the series which it follows. For example, PEI-1 is the postejaculatory interval following the first ejaculation.

The changes that occur over series leading up to sexual exhaustion have been described by Beach and Jordan (1956), Larsson (1956), Dewsbury (1968), and Karen and Barfield (1975). The major feature of this process is a steady lengthening of the PEI with each succeeding series. Changes also occur in EL, MIII, and IF near the beginning and the end of the sessions. EL-2, MIII-2, and IF-2 tend to be less than in the first series, and the decreased values are generally maintained in succeeding series. A dramatic increase is found in EL and MIII in the last series or two before the satiety criterion is reached. A smaller increase is found in late series in IF (Dewsbury, 1968; Karen & Barfield, 1975). Karen and Barfield (1975) further analyzed PEI into two components: an absolutely refractory post-ejaculatory period and a relatively refractory postejaculatory period following it. Both components were found to increase over series, but at different rates.

Review of Data on Recovery from Satiety

While the basic copulatory pattern and the changes that occur as satiety approaches have been systematically investigated and well described, this is not the case for the changes that occur as satiety dissipates. Results of early studies provided an outline of the process, but the course of recovery from sexual satiety has not yet been definitively described.

Stone and Ferguson (1940) noted that sexual activity on the second of two successive nights was considerably less than on the first in every rat they observed. "The period for recovery from copulatory satiation is much longer than that for either food or water satiation," they reported. "Data now on hand suggest that from approximately 4 to 6 days (possibly more) are required for recovery from a 2 hour period of unrestricted copulation to the degree that the average copulatory frequency on the second 2 hour period will closely approximate that of the first. The rate of recovery has not yet been fully worked out" (Stone & Ferguson, 1940, pp. 429-430).

In his classic monograph Larsson (1956) reported some observations on recovery from partial satiety. Sexually experienced rats were observed in 1-hr copulatory sessions (1) after one month of rest, (2) after copulating for 1 hr every 4 days for 12 days, (3) after copulating for 1 hr every 3 days for 12 days, and (4) after one month. Each subject was observed under each of these conditions in order. Normally about 50% of the rested males copulating in a 1-hr test achieve five or more ejaculations, thus the 1-hr timed test may be considered very roughly approximate to a test carried out to a criterion of satiety.

Larsson reported that activity in conditions (2) and (3) showed influences of sexual satiation, as compared with conditions (1) and (4). The effect was stronger in the

third condition (copulation every 3 days) than in the second (copulation every 4 days). The primary change was a great prolongation of PEI as compared with rested values for the same series. In another experiment Larsson (1956) observed the last of five daily 1-hr sessions of copulation. The increase in PEI was even more pronounced under these conditions. Larsson demonstrated that 14 days were sufficient for complete recovery from the satiety induced by daily 1-hr sessions.

In these and other experiments Larsson (1956) found the general effect of incomplete recovery from satiety or near-satiety to be (1) great prolongation of PEI, (2) fewer ejaculations obtained in 1 hr, (3) slight but reliable increases in MIII (measured as decreases in the rate of introduction), (4) a tendency for increase in EL, (5) no change in IF, and (6) some increases in MF (described as "incomplete attempts"). Larsson pointed out the similarity between these changes and those that occur within a session as satiety develops.

Schwartz (1956) compared an instrumental response (bar-pressing) and a consummatory response (copulation) as measures of sexual motivation in tests of fully rested rats and in tests after different periods of recovery. He stated: "On the basis of preliminary tests with a group of nonexperimental males and the published report of Stone and Ferguson (1940) it was concluded that six days of rest would

permit full recovery from a session of unlimited copulation and ejaculation" (Schwartz, 1956, p. 324). Schwartz trained 12 male rats to press a bar on a variable-interval schedule of reinforcement to obtain a receptive female for a single intromission. Tests were terminated when sexual satiety occurred as measured by a set of criteria involving both barpress responses and copulatory responses (intromissions), and subjects were retested after 1, 3, and 6 days of recovery. Schwartz found that recovery of the copulatory response varied directly with the length of time allowed for recovery following previous sexual exhaustion. Rate of barpressing was an insensitive measure of sexual recovery but was significantly correlated with changes in the copulatory pattern as satiety approached.

Beach and Jordan (1956) designed a systematic investigation of the course of sexual exhaustion and recovery in the male rat. Whereas Larsson used a timed test and Schwartz used a set of criteria complicated by barpress requirements, Beach and Jordan continued each test until 30 min elapsed without a mount. Whereas Larsson's design made it difficult to assess the degree of exhaustion with which a subject began or ended a test, Beach and Jordan preceded each test with a period thought to allow complete recovery, continued each test to a standard criterion of exhaustion, and tested the same subjects again after specific periods of recovery. Whereas in Schwartz' study the opportunity to

obtain an intromission was contingent upon prior barpress behavior, Beach and Jordan measured ad lib interintromission intervals.

The original design of the Beach and Jordan study involved three satiety tests which occurred after 6 days of rest from previous sexual satiety. One of these tests was followed by a retest after 1 day, while another was followed by a retest after 3 days. Twelve subjects received each of these five tests in different orders.

In the course of the experiment the authors began to suspect that a period of 6 days was not sufficient to allow complete recovery from sexual exhaustion. Accordingly, when the experiment described above was completed, the rats were given a 15-day rest and retested. Half the subjects were then tested again after 1 day, and half tested again after 3 days.

Although they performed no tests of significance, Beach and Jordan presented recovery data for four rest intervals: 1, 3, 6, and 15 days. Like Larsson, they found a decreased EF and longer PEIs in males not fully recovered. Most of their subjects did not copulate after only 1 day of rest since satiety. EL-1 was increased after both 3- and 6-day recovery intervals, but EL in later series did not appear to be different. PEIs for every series were longer after 6 days of rest than after 15 days and longer after 3 days than after 6. "A curve drawn through the median values [of EF]

for days 1, 3, 6, and 15," Beach and Jordan proposed, "would show that sexual recovery is a negatively accelerated function and is probably complete at some point between the tenth and fifteenth days of rest" (Beach & Jordan, 1956, p. 126).

Beach and Jordan's results indicated that the process of recovery from satiety takes considerably longer than previously thought. Because of this, their study did not include observations at all relevant stages of the process, and the length of the recovery period was not accurately determined.

In addition, one of the advantages of their design, mentioned above, was negated by pooling the data from the two phases of the experiment. In the second phase, 1-day and 3-day recovery periods were counted from satiety that was incurred in fully rested animals. In the first phase, however, tests after 1-day and 3-day recovery intervals were made following satiety that was incurred in males that had gained what was apparently only partial recovery from previous activity (i.e., the satiety session was preceded by 6 rather than 15 days). Larsson found, under the conditions of his procedures, an intensification of the satiation effects with repeated testing, as described above. It is not known to what extent, if at all, sexual exhaustion may accumulate when tests are continued to a criterion of exhaustion and complete recovery is not allowed between repeated tests. We cannot be sure, therefore, that the level of

satiety from which recovery was measured was controlled in the Beach and Jordan experiment.

The lack of statistical tests was another feature which limited the comparative value of their report. Their study did establish, however, that a period of 15 days is at least sufficient for full recovery of baseline levels of behavior, and in the 19 years since this classic study appeared, researchers planning experiments have routinely allowed 14-15 days for recovery from sexual satiety in the male rat.

Some confirmation of Beach and Jordan's results was supplied in a recent study of sexual satiety in the rat (Karen & Barfield, 1975). Karen and Barfield gave recovery tests 3 days after satiety and 6 days after satiety, with the satiety session preceding each test preceded by 2 weeks of rest since previous activity. They found an influence of satiety on EF and PEI still present after 6 days, but they did not measure intervals between 6 days and 2 weeks.

Such an extended period of recovery from satiety constitutes an interesting phenomenon, in that few biological systems of this sort require so long a period to recover from use. It is difficult to see how depletion of resources in a satiety test can be so great that two weeks without sexual activity is required to reinstate rested levels of behavior.

The closest-related species for which recovery data are available, the golden hamster (Mesocricetus auratus),

appears to attain complete recovery from sexual satiety within 5 days (Beach & Rabedeau, 1959). A number of characteristics of the copulatory pattern in hamsters are quite similar to the pattern in rats. Hamsters show the same combination of key features--multiple intromissions, multiple ejaculations, no thrusting during intromission, and no lock--which define pattern 13 in Dewsbury's classification system (Dewsbury, 1972). Like rats, hamsters show a decrease in IF and MIII after the first series, and an increase over series in PEI. Beach and Rabedeau found that while hamsters tend to copulate at a faster rate than rats (shorter MIII and PEIs) and they achieve a greater number of ejaculations ($EF = 9$), they still appear to obtain full recovery from satiety much faster than rats (about 5 days). This comparison, while it affords no basis for conclusions, serves to emphasize the question why the process of recovery from sexual satiety in male rats should require so long a period.

The Present Study

It is clear that a more detailed determination of the course of recovery from sexual satiety is warranted. Such a determination will be directly relevant to an understanding of the satiety process and hence to any theoretical attempt to explain it. The information will also be of considerable practical value for experimenters using satiety tests in

studies of the effect of hormones, drugs, brain lesions or other physiological interventions, or any other experimental manipulations on sex behavior in rats.

The present experiment was undertaken as a normative study, to chart precisely the course of recovery from sexual satiety in male rats (Rattus norvegicus). All tests were continued to a criterion of satiety, 30 min without an intromission, the standard criterion currently used by most investigators. Because of great individual differences but relatively stable intraindividual patterns, this experiment, like previous studies, employed a within-subjects design. Each subject was tested after six different periods of recovery from satiety, particularly in the interval in which Beach and Jordan suggested that recovery becomes complete. In order to standardize the level of satiety from which recovery was measured, subjects were allowed complete recovery from previous activity and then satiated prior to each recovery test.

METHOD

Subjects

The subjects were 24 male Long-Evans rats. They were selected, according to the criteria given below, from a pool of 32 males with no prior copulatory experience. The rats were purchased at the age of 80 days from Blue Spruce Farms, Altamont, New York. They were a mean of 98 days old at the time of the first satiety session, and 240 days old at the time of the last test.

Subjects were housed individually in 17.8 x 25.4 x 17.8 cm Wahmann hanging cages in the room in which they were tested. A 12:12 hr reversed light-dark cycle prevailed, with lights off at 1100 hr and on at 2300 hr. Purina Lab Chow and water were continuously available.

Forty-eight females of the same age and strain were maintained in group cages in the same room and were fed the same diet. Eight groups of six females were rotated for use in mating tests throughout the experiment.

Apparatus

Four cylindrical plexiglass arenas, 66 cm high and 84 cm in diameter, were used for observing copulatory behavior. These were placed on wooden platforms, and the floor covered

with absorbent litter material. Observations were recorded manually on an Esterline-Angus event recorder.

Procedure

Preliminary handling.--At approximately 80 days of age, males were earpunched for identification. On each of the next five days each male was allowed to remain alone in an observation arena for 10-15 min.

Test procedures.--Tests were conducted in dim light during the last third of the dark phase of the (reversed) light cycle. Each male was given 3-5 min in the arena before a female was introduced. In satiety tests males copulated ad lib to the satiety criterion of 30 min without intromission. In the event that no intromission occurred in the first 15-20 min of the test, the test was terminated.

Females were brought into behavioral estrus for copulatory tests through intramuscular injections of 0.1 mg estradiol benzoate in oil approximately 75 hr before testing and 1.0 mg progesterone in oil 3-4 hr before testing. Only those females exhibiting good receptivity when checked with a nonexperimental male immediately before a test were used in actual testing.

Pretesting.--Pretesting was begun after completion of preliminary handling. Each male was given one to three opportunities to mate with a receptive female. Pretests were terminated after the second ejaculation or after 15 min if copulation did not take place. A male that did not

achieve intromission within 15 min was given a second pre-test two days later. Some of those that failed to copulate both times were given a third opportunity several days later.

In this way 24 males were selected as subjects on the basis of having demonstrated successful copulation. Each subject then was allowed to copulate to satiety two weeks prior to the start of the experiment in order to insure stabilization of the effects of experience.

Design of the experiment.--Copulatory behavior was observed after various periods of recovery from sexual exhaustion. The exhaustion from which recovery was measured was established in a nonexperimental satiety session preceding each experimental test. Thus, each experimental condition actually involved two sessions--one to establish satiety and the other, a certain number of days later, to measure recovery.

The experimental tests were conducted after 3, 6, 9, 11, 13, or 15 days of recovery. Each subject was tested under each of these conditions. Subsequent to the initial satiety experience, each subject copulated to satiety 12 times in the course of the experiment. The experimental tests and the satiety sessions preceding them were identical in every respect except for the length of the rest interval since previous sexual activity. The period elapsing after a test before the nonexperimental satiety session preceding

the next test was the standard two-week period normally allowed for full recovery from satiety.

Six groups of four subjects received the six experimental conditions in different orders. A randomly selected 6 x 6 Latin square provided a randomized, counterbalanced running order, so that each condition appeared first for one group, second for another, and so on (Winer, 1972, p. 693). The actual orders used appear in Table 1.

A running schedule was devised to fulfill the requirements of the six groups in such a way that all 312 satiety tests were conducted in the space of five months.

Table 1
Running Orders

Group	Test					
	1st	2nd	3rd	4th	5th	6th
A	3	11	13	6	9	15
B	15	9	6	13	11	3
C	9	15	11	3	13	6
D	11	6	15	9	3	13
E	6	13	3	111	15	9
F	13	3	9	15	6	11

Note. Entries are the six experimental conditions, representing days of recovery from sexual satiety. Each test was preceded by a nonexperimental satiety session.

RESULTS

For three measures, EF, ML, and IL, data consisted of one score per subject per session. For the remaining measures, MF, IF, EL, MIII, and PEI, data consisted of one score per subject per series in each session. Since subjects completed varying numbers of series before reaching satiety, not all the data could be analyzed in a within-subjects design. Three series were the maximum that could be analyzed in this experiment with all subjects and tests represented. Data were analyzed for 18 subjects for which data were essentially complete to a minimum of three ejaculations on each test. Of the original 24 subjects, four died before completion of the experiment, and two others had occasional negative tests resulting in a prohibitive number of missing data points.

All measures except ML and IL were subjected to least squares analyses of variance with repeated measures, yielding F ratios for the effect due to groups (representing running orders), for recovery interval, and for the groups-by-recovery interaction (Barr & Goodnight, 1972; Cohen, 1968). Individual comparisons were made using the ratio of the difference between means to the standard error of the difference (Winer, 1971, p. 603; Bruning & Kintz, 1968, p. 113).

Ejaculation Frequency

Mean EF values for each recovery interval are given in Table 2. Subjects attained fewer ejaculations after both the 3-day period and the 6-day period than after longer intervals, but only the Day 3 EF was significantly different, at least at the .05 level, from the Day 15 value (Table 2). These individual comparisons were made following an analysis of variance that showed a significant difference among recovery intervals (Table 3), but the analysis showed no differences among groups in the number of ejaculations achieved and no difference among groups in the effect of a given recovery interval on EF (groups-by-recovery interaction).

Mount Latency and Intromission Latency

The distributions of both ML and IL were extremely skewed. Most subjects took only a few seconds to begin copulation, but occasionally much longer latencies were recorded, up to the maximum of 900 sec imposed by the 15-min time limit. Table 4 gives medians, means, and standard errors for these two measures. The departure from normality of the distributions can be appreciated from the discrepancy between medians and means and from the size and heterogeneity of the standard errors of the means.

The scores for both ML and IL, therefore, were analyzed using the Friedman test, a two-way analysis of variance by ranks (Conover, 1971). A significant difference among recovery intervals was found in ML, but not in IL (Table 4).

Table 2
Ejaculation Frequency--Medians,
Means, and Standard Errors

Days of Recovery	Median	Mean	s.e.
3	4.3	4.1 ^a	0.4
6	5.7	5.9	0.4
9	6.5	6.7	0.4
11	6.5	6.4	0.6
13	6.3	6.3	0.4
15	6.2	6.3	0.5

Note. n = 18.

^aDiffers from Day 15, $p < .001$; t test.

Table 3
Ejaculation Frequency--Summary
of Analysis of Variance

Source	Sum of Squares	df	Mean Square	F	p
Regression	299.88	47			
Groups	35.05 ^a	5	7.01	<1	NS
Subjects within groups	115.41 ^a	12	9.62		
Recovery	78.84 ^a	5	15.77	6.12	<.001
Groups x Recovery	71.96 ^a	25	2.88	1.12	NS
Error within	154.67	60	2.58		
Corrected total	454.55	107			

^aCorrected (partial) sum of squares.

Table 4

Latencies (in seconds) To Begin Copulation--
Medians, Means, and Standard Errors

Days of Recovery	Mount Latency ^a			Intromission Latency ^b		
	Median	Mean	s.e.	Median	Mean	s.e.
3	13.0 ^c	22.7	7.0	20.5	58.4	18.9
6	11.0	11.7	1.3	17.5	22.2	3.7
9	11.1	47.3	37.2	13.2	67.7	49.1
11	11.5	10.7	.6	15.5	44.1	23.8
13	11.2	11.2	.8	16.5	56.2	33.6
15	10.0	10.7	.9	13.0	19.0	4.0

Note. n = 18.

^a $\underline{T} = 12.8$, $\underline{p} < .025$, Friedman test.

^b $\underline{T} = 7.3$ (NS), Friedman test.

^cDifferent from Day 15 scores, $\underline{T} = 8.0$, $\underline{p} < .005$; Friedman test.

Individual comparisons were made by further application of the Friedman test to the data for the recovery intervals being compared (Conover, 1971). Of the 18 subjects, 14 had longer latencies to the first mount in the test after the 3-day recovery interval than they did after 15 days. This difference in ML after 3 and 15 days of recovery was statistically significant, while the remaining comparisons (with Day 15) were not significant (Table 4).

Mount Frequency

Table 5 shows the mean mount frequencies for the first three series in tests after different periods of recovery from satiety. MF-2 and MF-3 were greater after 3 days of recovery than they were after longer recovery periods. The significant differences between 3-day and 15-day values for MF-2 and MF-3 are indicated in Table 5. Table 6 gives the analyses of variance for these measures.

The analysis of MF-1 showed that the number of mounts occurring in the first series did not change with different recovery intervals (Table 6). Even though the mean MF for the first series of the test after a 3-day period of recovery was greater than after other periods (Table 5), this apparently did not reflect a consistent trend within subjects.

Intromission Frequency

The number of intromissions obtained in a given series was extremely stable. Means for tests after 3 days of

Table 5
Mount Frequency, Series 1, 2, and 3--
Means and Standard Errors

Days of Recovery	MF-1		MF-2		MF-3	
	M	s.e.	M	s.e.	M	s.e.
3	8.7	1.8	5.2 ^a	1.1	6.5 ^b	2.2
6	5.0	0.9	2.4	0.8	3.4	1.1
9	5.1	0.9	2.1	0.6	3.6	1.0
11	5.0	0.9	2.7	0.6	4.6	1.5
13	6.1	1.6	1.9	0.5	1.9	0.7
15	6.2	1.8	3.1	1.0	1.9	0.6

Note. n = 18.

^aDifferent from Day 15, $p < .05$; t test.

^bDifferent from Day 15, $p < .01$; t test.

Table 6
Mount Frequency, Series 1, 2, and 3--Summary
of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>MF-1</u>					
Regression	2,124.87	47			
Groups	597.20 ^a	5	119.44	1.58	NS
Subjectswithin groups	909.47 ^a	12	75.79		
Recovery	191.59 ^a	5	38.32	1.47	NS
Groups X Recovery	435.86 ^a	25	17.43	<1	NS
Error within	1,560.12	60	26.00		
Corrected total	3,684.99	107			
<u>MF-2</u>					
Regression	759.97	47			
Groups	87.33 ^a	5	17.47	<1	NS
Subjectswithin groups	331.39 ^a	12	27.62		
Recovery	136.59 ^a	5	27.32	3.78	<.005
Groups X Recovery	217.76 ^a	25	8.71	1.21	NS
Error within	433.11	60	7.21		
Corrected total	1,193.07	107			
<u>MF-3</u>					
Regression	1,909.29	47			
Groups	43.71 ^a	5	43.71	<1	NS
Subjectswithin groups	49.65 ^a	12	49.65		
Recovery	74.75 ^a	5	74.75	3.06	<.02
Groups X Recovery	33.40 ^a	25	33.40	1.37	NS
Error within	1,464.71	60	24.41		
Corrected total	3,374.00	107			

^aCorrected (partial) sum of squares.

recovery (Table 7) suggest not the slightest influence of previous satiety. Analyses of variance for IF-1, IF-2, and IF-3 (Table 8) yielded no significant effect due to recovery intervals.

Ejaculation Latency

Increases in the time required to achieve ejaculation were found after a 3-day period of recovery for each of the first three series. Lengthening of EL was perhaps more pronounced in Series 2 and 3 than in the first series, but comparisons of Day 3 with Day 15 for all three series were statistically significant (Table 9). These comparisons were made following a significant effect due to recovery interval in analyses of variance for each measure (Table 10).

Mean Interintromission Interval

The average interval between intromissions was calculated for each series of each session for each subject. Mean MIIIs over subjects for each recovery interval are shown in Table 11. MIII showed the same general pattern of differences that was seen in MF. The analyses of variance (Table 12) demonstrated a significant recovery interval effect on MIII-2 and MIII-3, but not on the spacing of intromissions in the first series. Individual comparisons of recovery intervals showed MIII-2 and MIII-3 after 3 days of recovery to be significantly longer than after 15 days (Table 11).

Table 7

Intromission Frequency, Series 1, 2, and 3--
Means and Standard Errors

Days of Recovery	IF-1		IF-2		IF-3	
	M	s.e.	M	s.e.	M	s.e.
3	10.3	0.7	5.4	0.5	5.1	0.5
6	10.6	0.8	5.1	0.3	4.9	0.4
9	10.3	0.6	5.2	0.4	4.9	0.5
11	10.2	0.8	5.3	0.6	5.4	0.6
13	9.5	0.8	4.7	0.3	5.2	0.4
15	10.8	0.9	4.6	0.3	4.7	0.3

Note. n = 18.

Table 8

Intromission Frequency, Series 1, 2, and 3--
Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>IF-1</u>					
Regression	769.04	47			
Groups	106.01 ^a	5	21.20	<1	NS
Subjects within groups	461.36 ^a	12	38.45		
Recovery	11.85 ^a	5	2.37	<1	NS
Groups X Recovery	178.25 ^a	25	7.13	1.22	NS
Error within	341.06	60	5.85		
Corrected total	1,120.10	107			
<u>IF-2</u>					
Regression	168.61	47			
Groups	22.43 ^a	5	4.49	<1	NS
Subjects within groups	70.59 ^a	12	5.88		
Recovery	10.96 ^a	5	2.19	<1	NS
Groups X Recovery	66.17 ^a	25	2.65	1.07	NS
Error within	148.16	60	2.47		
Corrected total	316.77	107			
<u>IF-3</u>					
Regression	166.25	47			
Groups	22.47	5	4.49	<1	NS
Subjects within groups	74.87	12	6.24		
Recovery	6.72	5	1.34	<1	NS
Groups X Recovery	63.09	25	2.52	<1	NS
Error within	193.71	60	3.23		
Corrected total	359.96	107			

^aCorrected (partial) sum of squares.

Table 9

Ejaculation Latency (in seconds), Series
1, 2, and 3--Means and Standard Errors

Days of Recovery	EL-1		EL-2		EL-3	
	M	s.e.	M	s.e.	M	s.e.
3	440.8 ^a	62.8	370.1 ^b	81.2	403.4 ^b	87.8
6	268.4	22.2	147.1	14.5	181.5	25.3
9	329.9	32.8	149.3	17.0	186.7	39.3
11	280.8	25.9	163.2	25.7	260.2	68.6
13	375.8	77.6	140.6	17.7	151.1	19.8
15	318.7	35.8	134.7	16.0	133.5	19.9

Note. n = 18.

^aDiffers from Day 15, $\underline{p} < .05$.

^bDiffers from Day 15, $\underline{p} < .001$.

Table 10
Ejaculation Latency, Series 1, 2, and 3--
Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>EL-1</u>					
Regression	2,816,423.08	47			
Groups	578,767.36 ^a	5	115,753.47	1.05	NS
Subjects within groups	1,326,887.58 ^a	12	110,573.97		
Recovery	405,258.01 ^a	5	81,051.60	2.90	<.02
Groups x Recovery	534,668.85 ^a	25	21,386.75	< 1	NS
Error within	1,676,439.17	60	27,940.65		
Corrected total	4,492,862.25	107			
<u>EL-2</u>					
Regression	1,899,631.79	47			
Groups	37,349.99 ^a	5	7,470.00	< 1	NS
Subjects within groups	751,409.22 ^a	12	62,617.44		
Recovery	717,556.90 ^a	5	143,511.38	5.95	<.001
Groups x Recovery	355,884.27 ^a	25	14,235.37	< 1	NS
Error within	1,446,910.53	60	24,115.18		
Corrected total	3,346,542.32	107			
<u>EL-3</u>					
Regression	3,156,839.14	47			
Groups	44,902.84 ^a	5	8,980.57	< 1	NS
Subjects within groups	1,501,351.40 ^a	12	125,112.62		
Recovery	994,954.59 ^a	5	198,990.92	4.88	<.001
Groups x Recovery	724,580.11 ^a	25	28,983.20	< 1	NS
Error within	2,446,291.10	60	40,771.52		
Corrected total	5,603,130.25	107			

^aCorrected (partial) sum of squares.

Table 11

Mean Interintromission Interval (in seconds), Series
1, 2, and 3--Means and Standard Errors

Days of Recovery	MIII-1		MIII-2		MIII-3	
	M	s.e.	M	s.e.	M	s.e.
3	44.8	6.5	55.5 ^a	7.3	78.3 ^a	13.1
6	26.1	1.7	29.4	2.6	38.5	4.8
9	33.0	3.7	28.8	2.6	36.0	5.0
11	30.9	5.3	32.7	5.3	42.8	7.4
13	36.3	5.1	29.4	3.1	31.5	5.7
15	43.8	14.1	27.2	3.5	29.7	4.8

Note. n = 18.

^aDiffers from Day 15, $p < .001$; t test.

Table 12

Mean Interintromission Interval (in seconds),
Series 1, 2, and 3--Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	P
<u>MIII-1</u>					
Regression	55,566.38	47			
Groups	2,245.43 ^a	5	449.09	< 1	NS
Subjects within groups	35,557.82 ^a	12	2,963.15		
Recovery	4,458.22 ^a	5	891.64	1.22	NS
Groups x Recovery	12,839.44 ^a	25	513.58	< 1	NS
Error within	43,902.03	60	731.70		
Corrected total	99,468.41	107			
<u>MIII-2</u>					
Regression	33,240.07	47			
Groups	926.59 ^a	5	185.32	< 1	NS
Subjects within groups	14,882.23 ^a	12	1,240.19		
Recovery	10,886.56 ^a	5	2,177.31	10.58	<.0001
Groups x Recovery	7,095.85 ^a	25	283.83	1.38	NS
Error within	12,343.08	60	205.72		
Corrected total	45,583.16	107			
<u>MIII-3</u>					
Regression	78,680.09	47			
Groups	877.84 ^a	5	175.57	< 1	NS
Subjects within groups	35,411.31 ^a	12	2,950.94		
Recovery	30,624.80 ^a	5	6,124.96	7.12	<.0001
Groups x Recovery	13,278.97 ^a	25	531.16	< 1	NS
Error within	51,592.39	60	859.87		
Corrected total	130,272.48	107			

^aCorrected (partial) sum of squares.

Postejaculatory Interval

PEI-1.--The length of the refractory period following the first ejaculation was significantly longer on Day 3 than on Day 15 (Table 13), while the corresponding comparisons for 6, 9, and 11 days were not different from 15 days. PEI-1 was, however, significantly longer after 13 days than after 15 (Table 13). The variability at this point (standard error of the mean = 55.7 sec for tests after 13 days) was also considerably greater than for other rest intervals. Scrutiny of individual records for that recovery interval revealed that the unusually high mean of 369.7 sec was primarily due to one typically high-scoring subject whose PEI after the first ejaculatory series in this test was 510 sec, an atypically high value even for him. In fact, 9 of the 18 subjects had longer first series PEIs on the Day 15 test than they did on the Day 13 test. When the Friedman test was applied to these data, it resulted in a $T = 0.056$, which is not significant.

PEI-2.--The PEI following the second ejaculation increased steadily with decrease in the length of the recovery interval, and the analysis of variance indicated this association was significant (Table 14). PEI-2 values after 3 days, 6 days, and 9 days of recovery were each significantly different from PEI-2 after 15 days (Table 13).

Measures of behavior beyond the third ejaculation were not included for analysis. Since PEI-3 extends to the

Table 13

Postejaculatory Interval, Series 1 and 2--
Medians, Means, and Standard Errors

	PEI-1			PEI-2		
	Median	Mean	s.e.	Median	Mean	s.e.
3	461.5	473.2 ^a	23.2	593.5	639.0 ^a	42.3
6	336.5	320.2	12.1	413.0	409.0 ^a	11.8
9	313.5	310.7	10.1	390.0	394.4 ^a	16.4
11	299.0	299.1	12.6	365.5	378.0	16.6
13	297.0	369.7 ^b	55.7	362.5	301.8	10.3
15	291.0	301.8	10.3	382.5	368.8	13.9

Note. n = 18.

^aDiffers from Day 15, $p < .001$, t test.

^bDiffers from Day 15, $p < .05$, t test.

Table 14
 Postejaculatory Interval, Series 1 and 2--
 Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>PEI-1</u>					
Regression	1,084,150.38	47			
Groups	78,368.70 ^a	5	15,673.74	< 1	NS
Subjects within groups	337,575.50 ^a	12	28,131.29		
Recovery	367,732.11 ^a	5	73,546.42	7.38	<.0001
Groups x Recovery	256,219.47 ^a	25	10,248.78	1.03	NS
Error within	597,870.83	60	9,964.51		
Corrected total	1,682,021.21	107			
<u>PEI-2</u>					
Regression	1,490,404.96	47			
Groups	7,587.24 ^a	5	1,517.45	< 1	NS
Subjects within groups	392,019.87 ^a	12	32,668.32		
Recovery	955,130.21 ^a	5	191,026.04	30.49	<.0001
Groups x Recovery	99,085.49 ^a	25	3,963.42	< 1	NS
Error within	375,956.71	60	6,265.95		
Corrected total	1,866,361.67	107			

^aCorrected (partial) sum of squares.

beginning of the fourth series, it did not exist for all subjects on every test.

In summary, rats tested after 3 days of recovery from sexual satiety obtained fewer ejaculations but showed no influence of prior satiety on the latency to the first intromission, nor on the number of mounts, the number of intromissions, or the average interval between intromissions, in the first series. The latency to the first mount, the latency to achieve the first ejaculation, and the first postejaculatory interval were significantly longer in the Day 3 test than after 15 days of recovery. In the second and third series, IF was again unaffected, but MF, EL, and MIII were all significantly longer on Day 3 than on Day 15, as was PEI-2.

After 6 days of recovery, EF was found to be somewhat less than after 15 days, but not significantly so. Recovery was complete on Day 6 in terms of every other measure except PEI-2, which was significantly longer on both Day 6 and Day 9 than on Day 15.

Supplementary Analyses

Data from the set of fully rested satiety sessions which preceded each test were examined for changes over time, since by the end of the experiment, subjects were five months older and considerably more experienced. The first time the subjects copulated to satiety was during the pretesting period, two weeks prior to the satiety

session which preceded the first test. This initial session was included for analysis. Thus a total of seven sessions were analyzed.

Each measure was subjected to an analysis of variance similar to those reported above for recovery data. Summaries of these analyses appear in the Appendix. Means for each session are given in Tables 15 to 20. The strongest effect was in EF, which decreased steadily with time (Table 15). This relationship was significant ($F = 9.30$, $df = 6,102$; $p < .001$). Every other measure showed an increase in value (great or slight) between the next-to-last and the last session and, in some cases, also between the antepenultimate and the penultimate. The measures for which test number constituted a significant effect, besides EF, were EL-1 and EL-2 (in both cases $F = 2.30$, $df = 6,102$; $p < .05$), MF-2 ($F = 2.40$, $df = 6,102$; $p < .05$), MIII-2 ($F = 2.26$, $df = 6,102$; $p < .05$), and MIII-3 ($F = 2.76$, $df = 6,102$; $p < .05$). Analysis of IF-1 also resulted in a significant difference among sessions ($F = 2.72$, $df = 6,102$; $p < .05$), but in this case the pattern of differences was not the same as that which the other measures showed. The other measures for which a significant difference was found showed relatively consistent values for the first six sessions, then an increase in the session preceding the last experimental test. The exception to this finding was EF, which decreased regularly from the first to the last

Table 15

Ejaculation Frequency--Means and Standard
Errors for Seven Satiety Sessions

	Session						
	1	2	3	4	5	6	7
Mean	8.7	7.5	7.2	7.1	6.4	6.1	5.6
s.e.	0.5	0.5	0.5	0.3	0.3	0.4	0.6

Note. n = 18.

Table 16

Postejaculatory Interval, Series 1 and 2--Means
and Standard Errors for Seven Satiety Sessions

		Session						
		1	2	3	4	5	6	7
PEI-1	M	326.1	303.2	293.3	300.1	287.7	313.3	368.7
	s.e.	10.7	9.0	6.7	13.3	41.8	11.5	50.9
PEI-2	M	388.8	380.8	386.4	381.5	358.1	359.2	403.9
	s.e.	10.5	17.5	16.6	20.3	11.1	13.0	23.1

Note. n = 18.

Table 17

Ejaculation Latency, Series 1, 2, and 3--Means
and Standard Errors for Seven Satiety Sessions

		Session						
		1	2	3	4	5	6	7
EL-1	M	344.4	368.9	295.9	304.2	302.9	395.4	489.6
	s.e.	40.3	76.6	27.4	45.7	31.3	46.8	85.6
EL-2	M	142.1	163.0	144.1	156.2	129.1	147.8	224.3
	s.e.	10.1	40.3	16.2	32.1	18.3	12.8	36.5
EL-3	M	236.8	177.0	224.6	138.2	150.0	177.9	376.8
	s.e.	94.0	52.3	46.3	15.8	19.2	32.7	133.2

Note. n = 18.

Table 18

Mount Frequency, Series 1, 2, and 3--Means and
Standard Errors for Seven Satiety Sessions

		Session						
		1	2	3	4	5	6	7
MF-1	M	4.8	3.6	3.8	4.3	4.3	5.8	6.3
	s.e.	1.0	0.6	0.6	0.8	0.7	0.9	1.7
MF-2	M	1.6	1.8	2.1	1.8	1.8	2.2	3.9
	s.e.	0.5	0.5	0.5	0.6	0.4	0.4	0.8
MF-3	M	4.4	1.9	3.9	2.0	2.1	2.1	7.9
	s.e.	2.8	0.5	1.1	0.4	0.5	0.6	3.4

Note. n = 18.

Table 19

Intromission Frequency, Series 1, 2, and 3--Means
and Standard Errors for Seven Satiety Sessions

		Session						
		1	2	3	4	5	6	7
IF-1	M	12.7	11.7	11.0	9.4	10.4	11.0	11.1
	s.e.	1.1	1.0	0.8	0.7	0.8	1.1	0.8
IF-2	M	5.3	5.1	5.3	4.7	5.0	5.3	5.6
	s.e.	0.3	0.3	0.5	0.4	0.3	0.4	0.4
IF-3	M	6.5	5.2	5.9	5.0	5.0	5.7	6.7
	s.e.	1.0	0.4	0.6	0.4	0.4	0.8	1.2

Note. n = 18.

Table 20

Mean Interintromission Interval, Series 1, 2, and 3--
Means and Standard Errors for Seven Satiety Sessions

		Session						
		1	2	3	4	5	6	7
MIII-1	M	27.2	35.1	28.5	34.1	29.0	34.9	44.6
	s.e.	2.9	8.8	3.3	5.7	2.1	3.3	7.0
MIII-2	M	27.5	30.5	27.1	31.7	27.1	29.2	39.3
	s.e.	2.2	4.8	1.6	3.8	2.2	2.5	5.7
MIII-3	M	30.9	31.8	37.9	27.6	30.7	31.1	56.7
	s.e.	4.2	5.8	7.3	2.6	3.6	2.9	14.2

Note. n = 18.

session. IF-1, on the other hand, was higher in the initial session than at other times and dropped to a lower value for the fourth session, in the middle of the experiment (Table 20).

DISCUSSION

The primary objective of this study was to determine how long the effects of sexual satiation on subsequent copulatory behavior persist in male rats. This objective was fulfilled and represents the first accurate determination of recovery from satiety in rats. Results of this study indicate that recovery from satiety is complete, as measured by every index, at least 4 days sooner than the 15 days investigators have customarily allowed. In fact, all measures of behavior from the initial mount up through the second ejaculation recovered their baseline values in this study by the sixth day after satiety. The pattern of recovery for each measure is summarized in Table 21.

Different measures recovered at different rates. As the table makes clear, recovery from satiety is a function of the measure used to define it. Ordinarily one would not wish to ascribe complete recovery to an animal which showed residual effects of satiety in any measure of copulatory behavior. By this criterion the earliest we can call recovery complete is after 11 days of rest. But there might well be practical instances in which only the within-series data (excluding PEI) of the first two or three series would be of interest. In these cases, copulation could be resumed

Table 21
 Recovery from Sexual Satiety in 17
 Measures of Copulatory Behavior

Measure	Days of Recovery					
	3	6	9	11	13	15
ML	0	x	x	x	x	x
IL	x	x	x	x	x	x
EF	0	x	x	x	x	x
IF-1	x	x	x	x	x	x
IF-2	x	x	x	x	x	x
IF-3	x	x	x	x	x	x
MF-1	x	x	x	x	x	x
MF-2	0	x	x	x	x	x
MF-3	0	x	x	x	x	x
EL-1	0	x	x	x	x	x
EL-2	0	x	x	x	x	x
EL-3	0	x	x	x	x	x
MIII-1	x	x	x	x	x	x
MIII-2	0	x	x	x	x	x
MIII-3	0	x	x	x	x	x
PEI-1	0	x	x	x	x	x
PEI-2	0	0	0	x	x	x

Note. Entries indicate recovery (x) or lack of recovery (0).

after a rest period of 6 days following satiety without bias to the results, and if for some reason, IF were the sole measure of interest, recovery might be considered to be complete after only 3 days.

Comparison with Results of Previous Studies

The major effects of prior exhaustion found in this study--a lengthening of postejaculatory intervals and a decrease in the number of ejaculations--have been consistently noted in previous studies. While each of these early studies contained flaws, as outlined earlier, comparisons with earlier data are of interest.

Postejaculatory interval.--The lengthening of PEI has been a pronounced effect at every recovery interval of less than 11 days ever measured. It was by far the strongest effect found by Larsson (1956). Beach and Jordan (1956) found an increase in PEI at 3 and 6 days of recovery for all series. Karen and Barfield (1975) found a statistically significant lengthening of PEI-1 at 3 and 6 days but did not compare PEI-2. In the present study no significant increase in PEI-1 was found beyond 3 days, but the differences found in PEI-2 extended this effect for the first time to a period of 9 days following satiety.

Ejaculation frequency.--The number of ejaculations achieved in tests after various intervals of recovery from satiety has been reported by Beach and Jordan (1956) and by Karen and Barfield (1975). Larsson's (1956) data on the

number of ejaculations achieved in a 1-hr test are not strictly comparable. Figure 1 shows mean EF values from the present study (for 3, 6, 9, 11, 13, and 15 days), from Beach and Jordan's study (for 1, 3, 6, and 15 days), and from the study of Karen and Barfield (for 3 and 6 days, and two measurements at 15 days). A similar figure was presented by Beach and Jordan showing individual data points. Beach and Jordan's suggestion, quoted earlier, was that a curve drawn through the medians would reach asymptote between 10 and 15 days. Medians for Beach and Jordan's data and for data of the present study were actually quite close to their respective means, and are not presented here. Karen and Barfield did not report medians for their data.

The mean EF at 3 days of recovery was significantly different from that at 15 days in Karen and Barfield's study and in the present study (Table 21). Beach and Jordan did not perform tests of significance.

Although the tendency toward reduced EF after 6 days of recovery has been consistently found, this effect has not been shown statistically significant, either in the present study or by Karen and Barfield. It is conceivable that a true and reliable difference of very small magnitude may exist. The power of a test to detect such a small difference would ordinarily be quite low unless the sample size were great (Cohen, 1969).

Intromission frequency.--The resistance of IF to change due to prior satiety is another consistent finding across

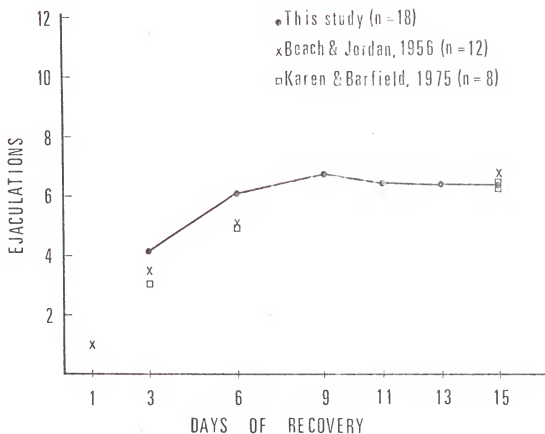


Figure 1. Mean ejaculation frequency after intervals of recovery from sexual satiety; data from three studies.

(Only rats which ejaculated at least once are included.)

studies (Larsson, 1956; Beach & Jordan, 1956; Karen & Barfield, 1975). The sole apparent exception occurs in the data of Beach and Jordan. They reported 8.2, 6.2, and 6.3 copulations per ejaculation for 3, 6, and 15 days, respectively. This apparently indicates an increase in IF after 3 days. Further analysis of these figures, however, resolves the apparent difference. The values reported are actually average intromission frequencies over all series. Since Beach and Jordan also reported that the normal copulatory pattern in fully rested rats involves a decrease from 10.6 intromissions in the first series to 6.0 in the second and slight further decreases in succeeding series, and since their Day 3 tests involved only an average of three series, it follows that the greater IF-1 value was more heavily represented in the average IF figure given for Day 3 than for later tests which involved five and six series. In fact, when the "copulations per ejaculation" figure is calculated on the basis of the fully rested IF values at each series and the Day 3 average IF, the result is 8.3. The apparent difference is thus resolved.

Other measures.--Results on IF and other within-series measures from the present study and three previous studies are presented in Table 22. The changes that have been found within series of copulations are not so pronounced as the effects discussed above, nor are these changes consistently

Table 22

Within-Series Measures After Incomplete Recovery
From Prior Satiety--Data From Four Studies

Measure	Larsson (1956) (n = 33)	Beach & Jordan (1956) (n = 12)	Karen & Barfield (1975) (n = 8)	The Present Study (n = 18)
IF-1	no change	no change	no change	no change
IF-2	no change	no change	---	no change
IF-3	no change	no change	---	no change
MF-1	--- ^a	increase	---	no change
MF-2	---	increase	---	increase
MF-3	---	increase	---	increase
EL-1	no change	increase	no change	increase
EL-2	(increase) ^b	no change	---	increase
EL-3	increase	no change	---	increase
MIII-1	increase	---	no change	no change
MIII-2	increase	---	---	increase
MIII-3	increase	---	---	increase

^a Increase reported in the number of mounts per hour.

^b Significant increase found in one experiment; no change found in another.

found. Larsson, for example, repeatedly described the effects he found in EL, in rate of intromission, and in the total number of mounts per hour as "slight."

The pattern of results across studies suggests that these weak effects might show up more easily in the second or third series than in the first series, in which values are already naturally higher. The exception to this is Beach and Jordan's finding that EL-1 was greater at 3 days but that EL-2 and EL-3 were not.

That an effect be more readily demonstrated in later series is a phenomenon frequently found in research on copulatory behavior. Dewsbury discussed this phenomenon in studies of the effect of experience (Dewsbury, 1969) and of drugs (Dewsbury & Davis, 1970; Dewsbury, 1971) and suggested that it might be related to greater variability in the first series than in later series. A relationship between series and strength of effect would be pertinent to the interpretation of studies which include only one copulatory series.

Like within-series measures, latencies to begin copulation have not shown entirely consistent results. These measures were not reported by Larsson or by Karen and Barfield. Beach and Jordan found increases in both mount and intromission latencies on Day 3, while in the present study, only ML was significantly affected. Mount and intromission latencies tend to be highly variable, since most scores

usually cluster about a minimum, while occasional scores might diverge extremely in one direction. The problem of variability in ML and IL has been discussed by Dewsbury (1975) in the context of comparative studies of adaptive significance.

Models of Copulatory Behavior

Beach (1956) proposed that sexual behavior in the male rat involves the operation of two different mechanisms. The arousal mechanism (AM) mediates the initiation and maintenance of sexual excitement. When the level of arousal reaches a certain threshold, the copulatory mechanism (CM) is activated. The execution of mounts, intromissions, and ejaculations is held to be dependent on the CM. The state of the AM should be reflected in mount and intromission latencies and postejaculatory intervals. Sexual satiety was described as a failure of arousal (Beach, 1956).

To account for their finding that copulation appears faster and more efficient (lower IF, EL, and MIII) in the second and subsequent series than in the first and their finding that PEI grows progressively longer, Beach and Jordan (1956) suggested that the first ejaculatory series has two effects: it sensitizes the CM (facilitating subsequent copulation), and it depresses the AM (cumulative action of which accounts for the lengthening of PEI).

Beach and Whalen (1959) investigated the duration of the facilitatory effects of the first ejaculation (or the

first series) on the subsequent series by removing the female for a period from 15 min to 7 hr after ejaculation. Because they found ML and IL on replacement of the female to be shorter than at the beginning of the first series, they proposed that the initial ejaculatory series stimulates both the CM and AM and that the lengthening of the PEI is due to nonsexual fatigue. That is, according to the revised model, the sensitization of the CM results in lower values for measures within the next series, as before, but nonsexual fatigue masks sensitization of the AM and produces a PEI. The fatigue wears off enough that the sensitized AM sparks the beginning of the next series and accounts for the shorter ML and IL on reintroduction of the female after an enforced PEI. Accumulation of the fatigue with each series causes the successive lengthening of PEI (Beach & Whalen, 1959).

That satiety should be attributable simply to buildup of fatigue is intuitively unsatisfying. Copulation does not seem so physically exerting that the effect of fatigue should still be present after 9 days of rest following sexual satiety, as found in the present study. Boland and Dewsbury (1971) found increases in sleep following sexual satiety in male rats, but of a different character and to a greater extent than they did following a comparable amount of exercise obtained from wheel running.

Further doubt was cast on the fatigue hypothesis by studies of prolonged PEIs early and late in extended

sessions of copulation (Dewsbury & Bolce, 1968; 1970). Prolongation of PEI-1 beyond the point at which the presumed fatigue has dissipated enough for the AM to activate the CM should result in less accumulation of fatigue and a shorter PEI-2 than usual. Dewsbury and Bolce (1970) found PEI-2 to be longer than usual. Prolongation of a PEI late in a satiety session should allow a lesser accumulation of fatigue to postpone the rat's reaching the satiety criterion. Dewsbury and Bolce (1968) found that a 1-hr PEI-4 (which normally would have been about 10 min and no longer than 30 min) produced instead a decrease in EF that was significant in one condition and not so in another.

The difficulty that prompted Beach and Whalen to propose fatigue in the first place was that ML and IL were shorter when the female was replaced after a prolonged PEI-1, whereas if the first series is supposed to depress the AM (to account for PEIs), it should have depressed these latencies as well. But there are alternative interpretations which do not necessitate the postulation of fatigue to explain satiety. The major alternative is the possibility that the initial latencies and PEI are not both controlled by the AM.

McGill (1965) has adduced some evidence that they are not, at least in mice, in that ML and PEI do not vary together across strains of mice. That is, a single strain

could have high values of one and low values of the other. The same lack of relationship can be noted in inbred strains of rats from data presented by Dewsbury (1975). Of four strains, the one with the highest ML and IL also had the shortest PEIs.

The model of rodent copulatory behavior proposed by McGill (1965) involves three processes. The arousal mechanism (AM), responsible for initiation of sex behavior, is sensitized by intromission and ejaculation. The copulatory mechanism (CM), activated by the first intromission, maintains excitement for a critical period of time until the threshold for ejaculation is reached. The CM is also sensitized by intromission and ejaculation. The third process is the ejaculatory mechanism (EM), discharged at ejaculation. Until a certain amount of recovery has occurred, this mechanism prevents the AM from operating, and the EM is progressively depressed if full recovery is not allowed between ejaculations.

Karen and Barfield have also proposed that three different processes underlie the three different rates of exhaustion found in their data. One rate was found for within-series measures, and two for the two components they distinguished within the PEI--the absolute refractory period (ARP) and the relative refractory period (RRP)(Karen & Barfield, 1975).

Based on observations of the behavior of males between series, Beach and Holtz-Tucker (1949) had suggested that the PEI was composed of two such phases. From a finding that

"superfacilitation" in the series of copulations resulted from PEIs prolonged just beyond normal length, Larsson (1959b) concluded that ejaculation is followed by an absolute, then a relative, refractory period and that ordinarily the next series begins during the RRP before recovery is maximal.

In work published since the present research was conducted, Barfield and Geyer (1974) discovered that the male rat emits ultrasonic vocalization during about the first 75% of the PEI and is unresponsive then to painful stimuli which, during the last quarter of PEI, could function to induce reinitiation of copulatory behavior. Defining an ARP and an RRP on the basis of the duration of vocalization, Karen and Barfield (1975) found different rates of exhaustion for the two components--linear increase for the ARP and postively accelerating for the RRP--as compared with a U-shaped function for EL, MIII, and IF. Thus, they proposed three processes at work.

The finding of the present study that a considerably slower rate of recovery from satiety is found in PEI than is found in other measures is consistent with all of the models discussed, since all assume the operation of at least two different processes or mechanisms. Two points of difficulty are raised, however, by the results of this study. The differences in the recovery patterns found in PEI and in ML and IL make one hesitant to ascribe both to the action

of a single mechanism, the AM. Beach and Whalen's (1959) finding that the effect of the first ejaculatory series on ML and IL was different from the effect on PEI might be explained on the basis that "ML" and "IL" on replacement of the female after an enforced PEI are not the same as the initial latencies. But the present study gives clearer indication that ML and IL do not behave in the same manner found in PEI.

The analysis of PEI into two components could conceivably resolve this discrepancy. It might be that Karen and Barfield's (1975) ART is reflecting what McGill (1965) termed the ejaculatory mechanism and that the RRP is subject to the AM as are the initial latencies. On the other hand, the satiation functions Karen and Barfield reported for the two refractory periods indicate that this is not a solution. The ART increases linearly with succeeding series at a low rate. It is the RRT which increases steeply as satiety approaches, supplying the characteristic shape of the PEI. Karen and Barfield also reported recovery data for these measures. The significant increase they found in PEI-1 on Day 3 and Day 6 was also found in the RRT alone, while the ART component had recovered by Day 6.

Thus the original problem remains of two measures supposedly reflecting the action of a single mechanism but behaving differently. It may be that the differences reflect some interaction of the effects of copulations and

ejaculations preceding the original satiety and of copulations and ejaculations occurring during the recovery test.

The second point raised by results of the present study is that while within-series measures are assumed to be controlled by the same mechanism, the CM, they do not appear to recover from the effects of satiety in a unitary fashion. Most measures showed increased values on Day 3 which decreased to normal on Day 6, but IF showed no increase at all on Day 3. It seems reasonable to suppose that the stability of IF in recovery tests reflects a faster recovery than seen for other within-series measures. None of the studies in which rats were observed after a 1-day recovery period reported IF values for this interval (Stone & Ferguson, 1940; Schwartz, 1956; Beach & Jordan, 1956). But IF does not seem to be as strongly affected by satiety as other measures. Even though IF shows a generally U-shaped function like the others (Karen & Barfield, 1975), the increases occurring as satiety approaches are not nearly so marked in IF as in EL and MIII (Dewsbury, 1968).

With respect to both points, it appears either that a single mechanism shows different effects in different measures or that the number of necessary mechanisms is greater than previously supposed. Future theoretical accounts should probably consider this question.

Change in Baseline over Time

An unexpected finding of this study was that copulatory behavior in fully rested animals changed over the course of the experiment. Fewer ejaculations, longer ejaculation latencies, longer intervals between intromissions, and more mounts without intromission were seen in the sessions establishing satiety near the end of the experiment than at the beginning. Several possible explanations suggest themselves.

Age.--Subjects in this experiment were aged 3 months (puberty) at the time of their first copulation to satiety and were 8 months old at the end of the study. Larsson and Essberg (1962) found differences in copulatory behavior between 3-month-old and 5 1/2-month-old males. However, these changes were in the direction of facilitation of the behavior, including an increase in EF and a decrease in EL. Likewise, Beach and Whalen (1959) found MF lower at 14 months of age than at 4 months. Larsson (1956) reported the highest sexual potency (EF in 1 hr) to occur at about 1 year of age. The effect found in the present study seems, therefore, to have occurred in spite of the increase in subjects' age, rather than because of it.

Experience.--Each subject experienced copulation to satiety a total of 13 times in the course of this investigation. Prior experience has been shown to produce small but reliable facilitating effects on almost all measures of copulatory behavior in male rats in the 3- to 6-month age

range (Dewsbury, 1969; Larsson, 1959a). Thus, it is difficult to attribute the decrements in copulatory behavior observed in the present experiment to either age or experience.

Accumulation of sexual fatigue.--Even though a male rat may copulate to satiety and show no residual effects in copulatory performance 15 days later, it is possible that a very slight influence of exhaustion remains which repeated testing may allow to accumulate and become visible. It is difficult to understand, however, what might be the nature of an influence that could persist for so long a period. This explanation seems even more unlikely in light of the results of the present study, showing recovery to be complete by 11 days following satiety. Nevertheless it remains an untested possibility.

Seasonal or cyclic fluctuations in sex behavior.--Most species show some seasonal changes in reproductive functions. Wild populations of Rattus rattus undergo a yearly cycle in which reproduction is lowest in the winter (Tamarin & Malecha, 1972). In his study of Rattus norvegicus in a controlled natural environment, Calhoun (1962) found that October to February was a period when young were not raised. He also reported seasonal variation in the descent of testes, which was not under the control of temperature. In the winter the testes of most males were retracted into the abdomen. From April through June almost all males were found with testes in the scrotum, and the proportion began

to decline in August (Calhoun, 1962). The present study was conducted during the months of April through August.

Although seasonal variation appears not to have been reported for Rattus norvegicus in the laboratory, it is not impossible for seasonal changes to persist even in a controlled environment. The white-footed mouse (Peromyscus leucopus), for example, continues to show seasonal changes in gonad function (Bartke & Chang, 1973) and in reproduction (Rood, 1966; Dewsbury, personal communication, 1975) even under constant laboratory conditions of temperature, lighting, and diet. The possibility of subtle seasonal changes in copulatory behavior in the laboratory rat is, therefore, plausible.

In any case this adjunctive result of the present study has raised a question which has potential significance for the interpretation of past and future research in copulatory behavior. It would seem to be worth pursuing experimentally.

Interaction of Long Term Changes with Recovery Effects

The demonstration of a change in behavior over time, whatever its origin might be, presents a potential confounding factor. If some influence was operating in this experiment to produce changes over time in the nonexperimental satiety sessions, that influence must also have been present during the experimental tests which alternated with them. However, the differential effect of occurring early

in the study or late in the study was balanced equally for all levels of the independent variable (recovery intervals) through the Latin-square procedure of randomizing running orders. Each of six recovery intervals occurred once at each of six time periods (first, second, . . . , sixth). The fact that not a single analysis of variance revealed the slightest interaction between recovery intervals and groups (running orders) demonstrates the efficacy of this design in controlling the effect of the time factor.

APPENDIX

Table A1

Ejaculation Frequency in Seven Nonexperimental
Sessions--Summary of Analysis of Variance

Source	Sum of Squares	<u>df</u>	Mean Square	<u>F</u>	<u>p</u>
Regression	361.31	23			
Session	115.36 ^a	6	19.26	9.30	<.0001
Subjects	245.75 ^a	17			
Error	211.30	102	2.07		
Corrected total	572.61	125			

^aCorrected (partial) sum of squares

Table A2

Ejaculation Latency, Series 1, 2, and 3 in Seven
Nonexperimental Sessions--Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>EL-1</u>					
Regression	3,055,058.20	23			
Sessions	518,608.83 ^a	6	86,434.80	2.30	< .05
Subjects	2,536,449.37 ^a	17			
Error	3,838,127.46	102	37,628.70		
Corrected total	6,893,185.66	125			
<u>EL-2</u>					
Regression	740,589.24	23			
Sessions	104,588.60 ^a	6	17,431.43	2.30	< .05
Subjects	636,000.63 ^a	17			
Error	773,120.25	102	7,579.61		
Corrected total	1,513,709.49	125			
<u>EL-3</u>					
Regression	2,965,609.27	23			
Sessions	713,051.52 ^a	6	118,841.92	1.54	NS
Subjects	2,252,557.75 ^a	17			
Error	7,883,856.19	102	77,292.71		
Corrected total	10,849,465.47	125			

^aCorrected (partial) sum of squares.

Table A3

Intromission Frequency, Series 1, 2, and 3, in
Seven Nonexperimental Sessions--
Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>IF-1</u>					
Regression	1,162.75	23			
Sessions	111.60 ^a	6	18.60	2.72	<.05
Subjects	1,051.14 ^a	17			
Error	696.97	102	6.83		
Corrected total	1,859.71	125			
<u>IF-2</u>					
Regression	107.47	23			
Sessions	9.52 ^a	6	1.59	< 1	NS
Subjects	97.94 ^a	17			
Error	193.33	102	1.90		
Corrected total	300.80	125			
<u>IF-3</u>					
Regression	356.17	23			
Sessions	51.75 ^a	6	8.63	1.03	NS
Subjects	304.42 ^a	17			
Error	855.97	102	8.39		
Corrected total	1,212.13	125			

^aCorrected (partial) sum of squares.

Table A4
 Mount Frequency, Series 1, 2, and 3, in
 Seven Nonexperimental Sessions--
 Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>MF-1</u>					
Regression	576.86	23			
Sessions	106.32 ^a	6	17.72	1.22	NS
Subjects	470.54 ^a	17			
Error	1,483.62	102	14.55		
Corrected total	2,060.54	125			
<u>MF-2</u>					
Regression	211.75	23			
Sessions	67.11 ^a	6	11.19	2.40	<.05
Subjects	144.64 ^a	17			
Error	475.75	102	4.66		
Corrected total	687.50	125			
<u>MF-3</u>					
Regression	1,877.51	23			
Sessions	527.63 ^a	6	87.94	1.71	NS
Subjects	1,349.87 ^a	17			
Error	5,257.79	102	51.55		
Corrected total	7,135.30	125			

^aCorrected (partial) sum of squares.

Table A5

Mean Interintromission Interval, Series 1, 2, and 3
In Seven Nonexperimental Sessions--
Summary of Analyses of Variance

Source	Sum of Squares	df	Mean Square	F	p
<u>MIII-1</u>					
Regression	23,890.70	23			
Sessions	3,831.95 ^a	6	638.66	1.68	NS
Subjects	20,058.74 ^a	17			
Error	38,851.86	102	380.90		
Corrected total	62,742.56	125			
<u>MIII-2</u>					
Regression	13,753.79	23			
Sessions	2,030.19 ^a	6	338.37	2.26	<.05
Subjects	11,723.60 ^a	17			
Error	15,250.93	102	149.52		
Corrected total	29,004.71	125			
<u>MIII-3</u>					
Regression	47,204.55	23			
Sessions	10,709.88 ^a	6	1,784.98	2.76	<.05
Subjects	36,494.67 ^a	17			
Error	65,968.72	102	646.75		
Corrected total	113,173.37	125			

^aCorrected (partial) sum of squares.

Table A6

Postejaculatory interval, Series 1 and 2, in
Seven Nonexperimental Sessions--
Summary of Analyses of Variance

Source					
<u>PEI-1</u>					
Regression	325,893.33	23			
Sessions	82,174.43 ^a	6	13,695.74	1.87	NS
Subjects	243,808.90 ^a	17			
Error	747,446.71	102	7,327.91		
Corrected total	1,073,430.04	125			
<u>PEI-2</u>					
Regression	277,836.87	23			
Sessions	28,988.63 ^a	6	4,831.44	1.45	NS
Subjects	248,848.23 ^a	17			
Error	340,811.94	102	3,341.29		
Corrected total	618,648.80	125			

^aCorrected (partial) sum of squares.

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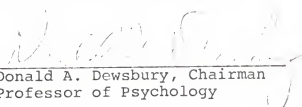
BIOGRAPHICAL SKETCH

Sally Jackson was born Sally Kendall Bolce in Oakland, California, January 21, 1943, and attended San Francisco Bay Area public and parochial schools until 1959. She graduated from Bishop Moore High School, Orlando, Florida, in 1960, and from Rollins College, Winter Park, Florida, in 1964.

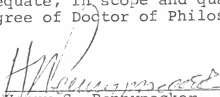
She attended the University of Florida from 1964 to 1968, receiving a master's degree in experimental psychology in 1967. After teaching for a year at Florida Southern College, Lakeland, Florida, she returned to the University of Florida in 1969 and completed data collection for this dissertation in 1971.

In 1972-73 Sally studied with Maharishi Mahesh Yogi in Arcata, California, and La Antilla, Spain, to become a teacher of Transcendental Meditation. She spent the next year and a half studying and working at Maharishi International University in Santa Barbara, California, and Fairfield, Iowa. At MIU she met Daniel Jackson, whom she married in December, 1974. Sally devoted 1975 to completing the dissertation, while living at Fenwick Free in historic St. Mary's County, Maryland. The Jacksons now live and work in Washington, D.C.

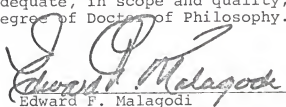
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Donald A. Dewsbury, Chairman
Professor of Psychology


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Henry S. Pennypacker
Professor of Psychology

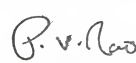
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Edward F. Malagodi
Associate Professor of Psychology

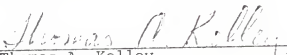
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Merle E. Meyer
Professor and Chairman of
Psychology

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P. V. Rao
Professor of Statistics

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Thomas A. Kelley
Assistant Professor of Statistics

This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1975

Dean, Graduate School